



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

Modeling daily energy balance of dairy cows in the first three lactations

Citation for published version:

Banos, G, Coffey, MP & Brotherstone, S 2005, 'Modeling daily energy balance of dairy cows in the first three lactations', *Journal of Dairy Science*, vol. 88, no. 6, pp. 2226-2237. [https://doi.org/10.3168/jds.S0022-0302\(05\)72898-8](https://doi.org/10.3168/jds.S0022-0302(05)72898-8)

Digital Object Identifier (DOI):

[10.3168/jds.S0022-0302\(05\)72898-8](https://doi.org/10.3168/jds.S0022-0302(05)72898-8)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Journal of Dairy Science

Publisher Rights Statement:

© American Dairy Science Association, 2005.

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.



Modeling Daily Energy Balance of Dairy Cows in the First Three Lactations

G. Banos,¹ M. P. Coffey,² and S. Brotherstone^{2,3}

¹Department of Animal Production, School of Veterinary Medicine, Aristotle University of Thessaloniki, GR-54124 Thessaloniki, Greece

²Sustainable Livestock Systems, Scottish Agricultural College, Bush Estate, Penicuik, Midlothian, EH26 0PH, United Kingdom

³Institute of Evolutionary Biology, University of Edinburgh, Ashworth Laboratories, King's Buildings, Edinburgh, EH9 3JT, United Kingdom

ABSTRACT

Daily energy balance was calculated for 111 Holstein cows in their first 3 lactations, based on combinations of smoothed preadjusted phenotypic records for milk yield, feed intake, live weight, and body condition score. Two energy balance traits were defined: one based on milk yield and feed intake (EB1) and the other on live weight and body condition score change (EB2). Bessel functions (BF), Legendre polynomials (LP), sinusoidal functions (SF), and cubic splines (CS) were used to model energy balance within and across lactations. Models with BF or LP fitted fixed regressions of order 1 to 6 and random regressions of order 1 to 10. Cubic splines were fitted at 5 to 30 equally spaced knot points. In within-lactation analyses with BF and LP models, likelihood ratio tests revealed that the fit improved significantly up to random regression order of 5 for EB1 and 4 for EB2, independently of the fixed regression order. For EB1 analyses with LP, improvement was marginal albeit significant even for higher random regression order. For CS models, optimal number of knot points was 13 and 12 for EB1 and EB2, respectively. Residual variance and comparisons between actual and predicted energy balance showed that LP of minimum order 8 and 5 modeled, respectively, EB1 and EB2 better than the other 3 functions. In across-lactation analyses with BF and LP models, likelihood ratio tests were significant as the random regression order increased, for any order of the fixed regression. For CS models, optimal number of knot points was 14 and 16 for EB1 and EB2, respectively. Residual variance and comparisons between actual and predicted energy balance showed that models fitting CS and high (>8) random order BF or LP provided the best fit to both traits. However, in an across-lactation analysis, even higher

order of LP or BF will be required to provide as good a fit as within-lactation analyses.

(Key words: energy balance, model functions, dairy cattle)

Abbreviation key: BF = Bessel functions, CS = cubic splines, EB1 = energy balance calculated from feed intake and milk yield, EB2 = energy balance calculated from changes in live weight and BCS, LP = Legendre polynomials, SF = sinusoidal functions.

INTRODUCTION

In dairy cattle it is important to ensure that individual animals get sufficient energy from feed intake to meet their physiological requirements. Dairy cattle need to produce milk, grow, conceive, and bring their calves to term, while maintaining themselves as biological entities, staying healthy, and keeping up with general activity.

The amounts of energy taken in and dispensed by a cow determine its body energy state. When current energy needs exceed current energy input, the cow is in negative energy balance. Body tissue (mostly as lipid reserves) is then heavily catabolized to offset energy requirements by various physiological activities. An animal in prolonged negative energy balance exhibits cumulative body energy loss and becomes prone to health and reproductive problems, and considerable financial loss (Beam and Butler, 1998; De Vries et al., 1999; Kendrick et al., 1999; Collard et al., 2000; De Vries and Veerkamp, 2000; Veerkamp et al., 2000).

Furthermore, carryover effects from one lactation to subsequent lactations frequently result in increasing negative energy balance and associated recurring health and fertility problems during a cow's productive life (Coffey et al., 2001). Given the relationship between energy balance and these functional traits, it follows that cows losing too much energy in a lactation and failing to gain enough back in the same lactation are predisposed to ill health and fertility in the following

Received October 22, 2004.

Accepted February 24, 2005.

Corresponding author: G. Banos; e-mail: banos@vet.auth.gr.

lactation, especially if the loss in that lactation pushes the cow's energy below some threshold. In addition, all lactating mammals tend to lose body energy to support lactogenesis, even more so when they are highly selected and highly producing Holstein cows (Coffey et al., 2004). Therefore, there must be an optimum rate of energy loss over the cow's productive life that maximizes milk production with an acceptable functional trait performance and life expectancy for the animal.

The energy profile of a cow changes over time, reflecting changes in its milk production, live weight, and BCS. Every one of these traits corresponds to one or more energy-demanding physiological activities. Live weight is associated with growth and pregnancy status, whereas BCS is associated with the level of metabolizable lipid reserves. Coffey et al. (2001) combined feed intake and milk yield data to calculate energy balance from direct energy input and output. They also combined live weight and BCS data for the same cows to calculate energy balance from predicted body lipid and protein weight changes.

In a breeding and genetic improvement program, it is desirable to understand the energy profile changes of animals under selection for yield, to identify cows that are genetically predisposed to retain energy and avoid lengthy intervals in a negative energy balance state. Furthermore, modeling and predicting the energy balance of a cow during its lifetime could become a useful management tool on the farm, assisting culling decisions, reproductive management, and other related practices.

As multiple energy balance records may be available on the same animal over time, modeling the trait becomes an exercise in repeated-measures analysis. The shape of the trait curve also needs to be taken into account. Coffey et al. (2002) considered sinusoidal functions to model and predict daily energy balance over 3 lactations of Holstein cows, achieving moderate accuracy and goodness of fit. De Vries et al. (1999) investigated several curves of early lactation energy balance and observed best fit with sixth-order polynomials and random regression models, followed closely by a modified Ali and Schaeffer function (Ali and Schaeffer, 1987).

Beyond parametric models, nonparametric approaches have also been used to analyze repeated observations and to model curves. Cubic splines have been used in this respect to model lactation and growth curves (White et al., 1999). Cubic splines are smooth curves formed by combining cubic polynomials at the so-called knot points. This results in the spline and its first 2 derivatives being continuous over the entire length of the curve (Green and Silverman, 1994). White et al. (1999) described the basic mathematical theory of cubic splines in an animal breeding context.

Outside the animal science field, energy state exhibiting cyclical patterns is frequently modeled using Bessel functions, which are defined as solutions of certain differential equations (Arfken, 1985). Bessel functions of any order can be expressed as a series of gamma functions. Applications of Bessel functions are found in various areas of physics including atomic ionization (Reiss and Krainov, 2003), energy transfer in thermodynamics (Roura et al., 2000), electromagnetism (Taylor, 1974), and acoustic waves (Leach, 1989). A desirable property of Bessel functions is that they are harmonic and asymmetrical; therefore, from an animal science standpoint, they might be effective at modeling varying rates of energy change (amplitude) and total energy content (phase) across individual cows.

The objective of this study was to evaluate 4 modeling functions of daily energy balance of dairy cows both within lactation and across their productive life in the first 3 lactations.

MATERIALS AND METHODS

Data

Data were collected from Holstein cows kept at the Langhill Dairy Cattle Research Centre in Scotland, between 1990 and 2002. These cows had been participating in feed and selection trials conducted at the Centre. Energy balance measures were obtained from adjusted phenotypic values for 4 other traits that were routinely recorded at the Centre. The traits were milk yield and fresh feed intake (recorded on each cow daily) and BCS and live weight (measured on each cow weekly). Milk yield was defined as the sum of the morning and evening yields, feed intake was calculated from the difference between food offered and food refused, BCS was expressed on a scale from 0 (thin) to 5 (obese), and live weight was measured after morning milking, at the same time as BCS. Records for these traits were analyzed with random regression models (Coffey et al., 2002). Each trait was analyzed separately. Models included the fixed effects of feed group, genetic line, time of measurement, percentage of North American Holstein genes, age at calving, and fourth-order Legendre polynomials of days of lactation, fitted within lactation (Coffey et al., 2002). Because a test-day model was implemented, daily solutions were derived for all traits, whether they had been recorded daily or weekly. Animal solutions per day of lactation obtained from these analyses were used to calculate daily values, on the phenotypic scale, for all 4 traits, for days of lactation 1 to 305 of the first 3 lactations of each cow. It should be noted that these days corresponded to 1 to 1431 d since the cow's first calving, representing days of productive life, where 1431 was the maximum number of produc-

Table 1. Descriptive statistics for daily energy balance calculated from feed intake and milk yield (EB1) and daily energy balance calculated from live weight and BCS changes (EB2).

Trait	Mean	SD	Minimum	Maximum
EB1 (MJ/d)				
Lactation 1	8.8	27.8	-103.1	137.4
Lactation 2	15.1	37.4	-131.0	176.1
Lactation 3	-1.5	42.8	-166.5	148.3
Across lactation	7.4	37.2	-166.5	176.1
EB2 (MJ/d)				
Lactation 1	4.7	18.9	-68.5	150.0
Lactation 2	7.7	22.3	-76.8	147.1
Lactation 3	6.7	22.8	-70.0	150.8
Across lactation	6.4	21.4	-76.8	150.8

tive days for a cow at the end of lactation 3. Daily adjusted phenotypic values for the 4 traits were then converted to energy equivalents using the effective energy system of Emmans (1994). Energy equivalents were combined to derive 2 separate energy balance traits. The first (**EB1**) was based on daily adjusted phenotypic values for milk yield and feed intake, and actual live weight records, and represented the direct balance emanating from energy available to a cow and requirements for production and maintenance. The second energy balance trait (**EB2**) was based on daily adjusted phenotypic values for live weight and BCS, and represented changes in lipid and protein weight over time. Coffey et al. (2001) described these procedures in detail.

All cows were required to have 3 complete lactations to ensure the energy balance profile was studied throughout productive life on the same animals. Cows were also required to be in milk for at least 305 d in every lactation and have all 4 traits (milk yield, feed intake, BCS, and live weight) continuously recorded. In total, 100,566 daily energy balance measures of 111 cows in their first 3 lactations were included in the study.

Models

Table 1 gives descriptive statistics for the 2 energy balance traits both within and across lactation, and Figure 1 illustrates the average EB1 and EB2 by day of lactation for the 3 lactations. A visual appraisal of the curves in Figure 1 reveals that cows started each lactation in negative energy balance and gradually regained body energy before returning to positive energy balance by approximately d 70. Cyclical patterns were observed across lactation, with each lactation cycle lasting on average 399 d (mean calving interval of the cows included in this study). An attempt to model energy balance curves should describe these fluctuations sufficiently and take into account the between-cow variance

in rate of regaining body energy and in total amount of energy gain/loss at the end of each lactation.

Coffey et al. (2002) considered sinusoidal functions (**SF**) suitable for describing the cyclicity of energy balance across a cow's productive lifetime. Sinusoidal functions were fitted in the present study using model 1 for within lactation analysis.

$$Y_{ijk} = (D_i)_k + \left(a + b_1 \sin\left(\frac{2\pi T_j}{mCI}\right) + b_2 \cos\left(\frac{2\pi T_j}{mCI}\right) \right)_k \quad [1]$$

$$+ \left(c_i + d_{1i} \left(\sin\frac{2\pi T_j}{CI_i} \right) + d_{2i} \left(\cos\frac{2\pi T_j}{CI_i} \right) \right)_k + e_{ijk}$$

where Y_{ijk} = daily energy balance (EB1 or EB2) record of cow i in lactation k ; D_i = fixed effect of number of weeks between d 305 and next calving, representing the milking period beyond d 305 and the dry period; T_j = day j of lactation k ranging from 1 to 305; CI_i = interval between calvings k and $k + 1$ of cow i ; mCI = average interval between calvings k and $k + 1$; a , b_1 , and b_2 = fixed regression coefficients associated with the overall curve; c_i , d_{1i} , and d_{2i} = random regression coefficients associated with cow i ; and e_{ijk} = random residual term. All effects were fitted within lactation k , ranging from 1 to 3.

The second type of function considered was the Bessel function (**BF**). Unlike SF, BF are asymmetrical; therefore, they may better account for varying amplitude and phase across animals. Bessel functions were fitted to daily energy balance records, within lactation, using model 2.

$$Y_{ijk} = (D_i)_k + \left(a + \sum_{n=0}^{nf-1} b_n B_n \left(\frac{2\pi T_j}{mCI} \right) \right)_k \quad [2]$$

$$+ \sum_{n=0}^{nr-1} c_{in} B_n \left(\frac{2\pi T_j}{CI_i} \right)_k + e_{ijk}$$

where Y_{ijk} = daily energy balance (EB1 or EB2) record of cow i in lactation k ; a and b_n = fixed regression coefficients associated with the overall curve; c_{in} = random regression coefficient associated with cow i ; B_n = n th BF of day j ; nf = fixed regression order ranging from 1 to 6; nr = random regression order ranging from 1 to 10; and other effects are as in model 1. All effects were fitted within lactation k ($k = 1, 2$, or 3). Bessel functions were programmed based on the modules described by Press et al. (1992). The general formula used for the n th BF of a real number x [$J_n(x)$] is given below:

$$J_n(x) = \sum_{k=0}^{\infty} \frac{(-1)^k}{k! \Gamma(n+k+1)} \left(\frac{x}{2} \right)^{(n+2k)}$$

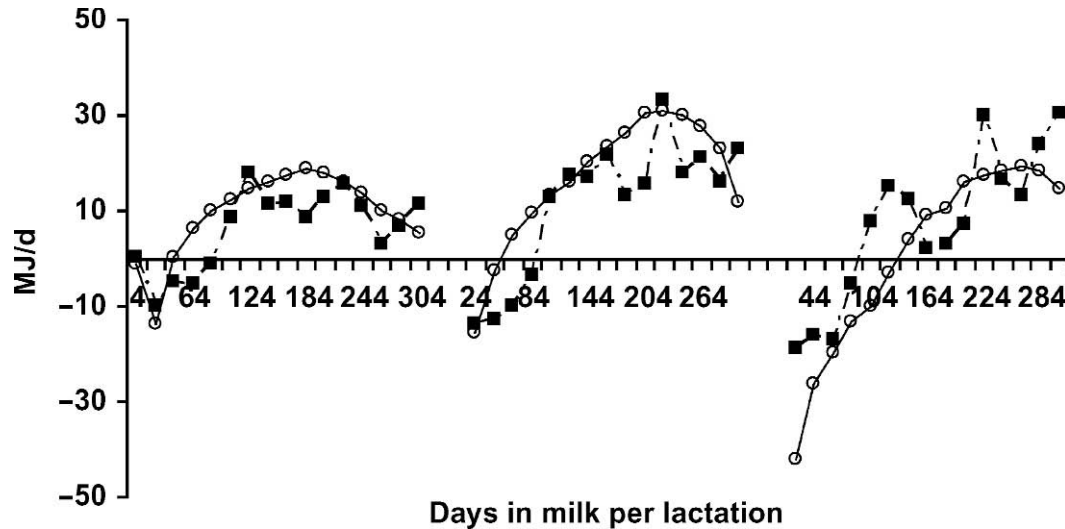


Figure 1. Average energy balance (EB1; ○) and energy balance change (EB2; ■) by day of lactation in the first 3 lactations.

where

$$\Gamma(n + k + 1) = \int_0^{\infty} e^{-x} x^{(n+k)} dx$$

Legendre polynomials (**LP**) were the third type of function considered in this study. These polynomials are routinely used in animal breeding for the analysis of repeated measures. They have a number of desirable properties including good convergence, simple usage, and orthogonality, meaning they yield correlation estimates between coefficients close to the “true” value. Legendre polynomials were fitted to energy balance records, within lactation, using model 3.

$$Y_{ijk} = (D_i)_k + \left(a + \sum_{n=0}^{nf-1} b_n P_n \left(\frac{2\pi T_j}{mCI} \right) \right)_k \quad [3]$$

$$+ \sum_{n=0}^{nr-1} c_{in} P_n \left(\frac{2\pi T_j}{CI_i} \right)_k + e_{ijk}$$

where Y_{ijk} = daily energy balance (EB1 or EB2) record of cow i in lactation k ; a and b_n = fixed regression coefficients associated with the overall curve; c_{in} = random regression coefficient associated with cow i ; P_n = n th LP of day j ; nf = fixed regression order ranging from 1 to 6; nr = random regression order ranging from 1 to 10; and other effects are as in model 1. All effects were fitted within lactation k ($k = 1, 2, \text{ or } 3$).

The final model fitted cubic splines (**CS**) to daily body energy balance measures. Cubic splines were fitted at 5 to 30 equally spaced knot points using model 4 for within lactation analysis.

$$Y_{ijk} = (D_i)_k + \left(a + b \frac{2\pi T_j}{mCI} \right)_k \quad [4]$$

$$+ \left(c_i + d_i \left(\text{spl} \frac{2\pi T_j}{CI_i} \right) \right)_k + e_{ijk}$$

where Y_{ijk} = daily energy balance (EB1 or EB2) record of cow i in lactation k ; a and b = fixed regression coefficients associated with the overall curve; c_i and d_i = random regression coefficients associated with cow i ; and other effects are as in model 1. All effects were fitted within lactation k ($k = 1, 2, \text{ or } 3$).

The radian term in all of the above functions was expressed in a way that aimed at capturing the cyclicity and periodicity of EB1 and EB2 in the first 3 lactations (Figure 1). There appeared to be 9 major inflection points in these curves (3 per lactation); therefore, BF and LP were fitted to a maximum regression order of 10. This should render the statistical results describing the trait curves biologically meaningful.

In a separate set of analyses with each one of the above 4 models, T was defined as the number of days since first calving, describing the actual length of productive life, ranging from 1 to 1431. In this case, energy balance was modeled across lactation and the other effects in the model were no longer nested within lactation.

All analyses were conducted with the ASREML software package (Gilmour et al., 2002). In all cases, the fit of each model was first evaluated by the log likelihood and the residual variance estimate. Further, the actual and predicted energy balance were compared using the root mean square error, the mean absolute difference, representing the average bias, and the product-moment

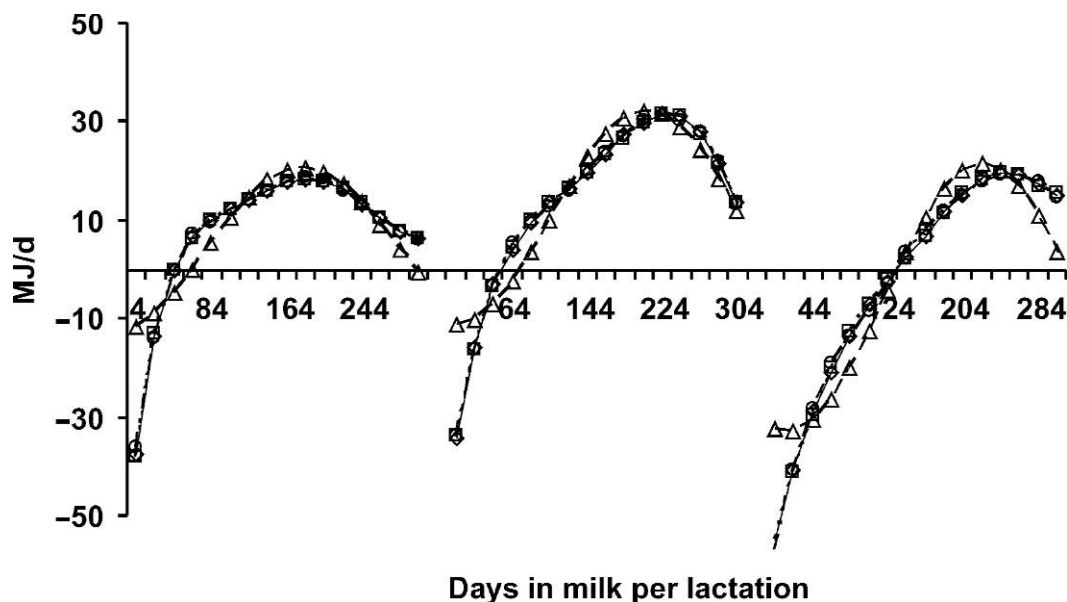


Figure 2. Average daily energy balance (EB1) predicted within lactation with Bessel functions (BF; \diamond), Legendre polynomials (LP; \square), sinusoidal functions (\triangle), and cubic splines (\circ); BF and LP fixed and random regression order = 6.

correlation squared, reflecting the proportion of total phenotypic variance explained by the model.

RESULTS

Within-Lactation Analysis

When the model included BF or LP, the log likelihood increased with the random regression order, independently of the order of the fixed effect. In the EB1 analysis, the likelihood ratio test of BF models was significant ($P < 0.05$) up to random regression order 5 and was always significant for LP models. However, in the latter, the improvement decreased considerably beyond the order of 5. In the EB2 analysis, the likelihood ratio test was significant ($P < 0.05$) up to random regression order 4 for both BF and LP models.

For CS fitting models, the optimal number of equidistant knot points was 13 and 12 for EB1 and EB2, respectively; these models were associated with the highest log likelihood and lowest residual variance. All CS results presented from this point onwards will refer to optimal number of knot points.

Figures 2 and 3 show the average fitted values of EB1 and EB2, respectively, for all models considered. Models fitting BF and LP with fixed and random order of 6 are used here for illustration. On average, BF, LP, and CS fitting curves were very similar to each other, whereas SF curves were slightly different. The former followed the plotted average data values (Figure 1) quite well.

Figures 4 and 5 show residual variance estimates of EB1 and EB2, respectively, when the model included sixth-order fixed regression on BF or LP and random regression on the same functions of order ranging from 1 to 10. Here fixed regression of sixth order is used for illustration purposes. Results were not affected by the order of the fixed regression. Residual variances of SF and CS fitting models are also shown in Figures 4 and 5. For EB1, residual variance was smallest ($P < 0.05$) when the model fitted LP of random order >7 , suggesting a better fit. Models fitting CS at 13 equally spaced points had similar residual variance to order 7 LP models, followed by lower order LP and BF models. The last 2 did not differ significantly from each other. Models fitting SF and single-order LP and BF had the largest residual variance. For EB2, residual variance was smallest for models fitting LP of order >4 , followed by CS (12 knot points), lower order LP, BF, and SF. Residual variance improved significantly ($P < 0.05$) when random BF order increased to 4 and random LP order to 6. Differences between LP and BF were significant ($P < 0.05$), in the favor of LP, when the random regression order in either case was >5 .

A very similar picture was painted by comparisons between predicted and actual daily body energy balance (Table 2 for EB1 and Table 3 for EB2). Comparison criteria included the root mean square error, the mean absolute difference, and the product-moment correlation squared. Models fitting LP of random regression order >7 and >4 were associated with the smallest (P

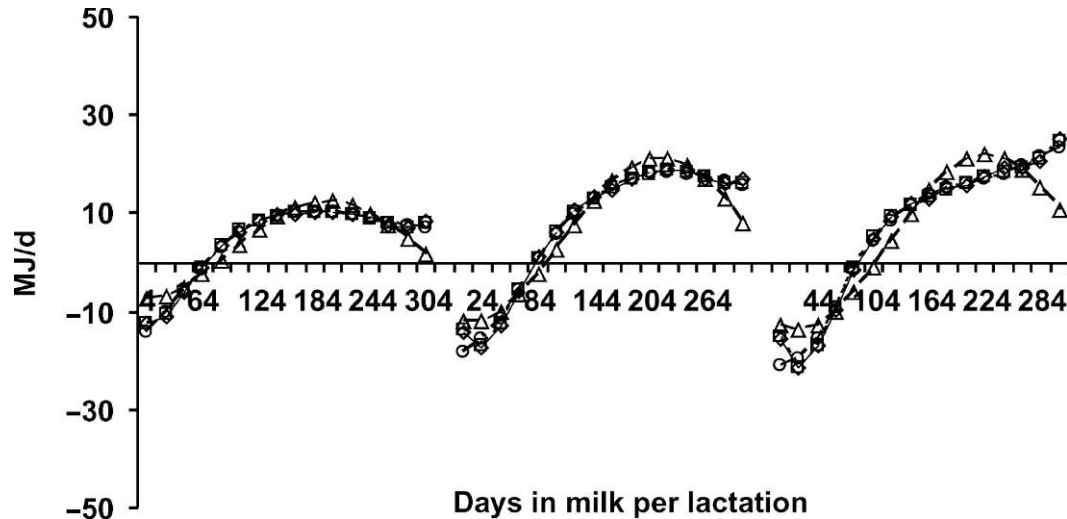


Figure 3. Average daily energy balance change (EB2) predicted within lactation with Bessel functions (BF; \diamond), Legendre polynomials (LP; \square), sinusoidal functions (\triangle), and cubic splines (\circ); BF and LP fixed and random regression order = 6.

< 0.05) root mean square error and average bias for EB1 and EB2, respectively. The same models explained the highest proportion of total phenotypic variance for EB1 (0.96) and EB2 (0.62). By the criteria considered in this study, all models fitted EB1 better than EB2.

Across-Lactation Analysis

When the model included BF or LP, the log likelihood increased significantly ($P < 0.05$) with the random re-

gression order (1 to 10), independently of the order of the fixed effect. The latter had trivial effect on any of the results of this study.

For CS models, the optimal number of equidistant knot points was 14 and 16 for EB1 and EB2, respectively; these models were associated with the highest log likelihood and lowest residual variance. As in within-lactation analysis, any reference to across-lactation CS results from this point onwards will refer to the optimum number of knot points.

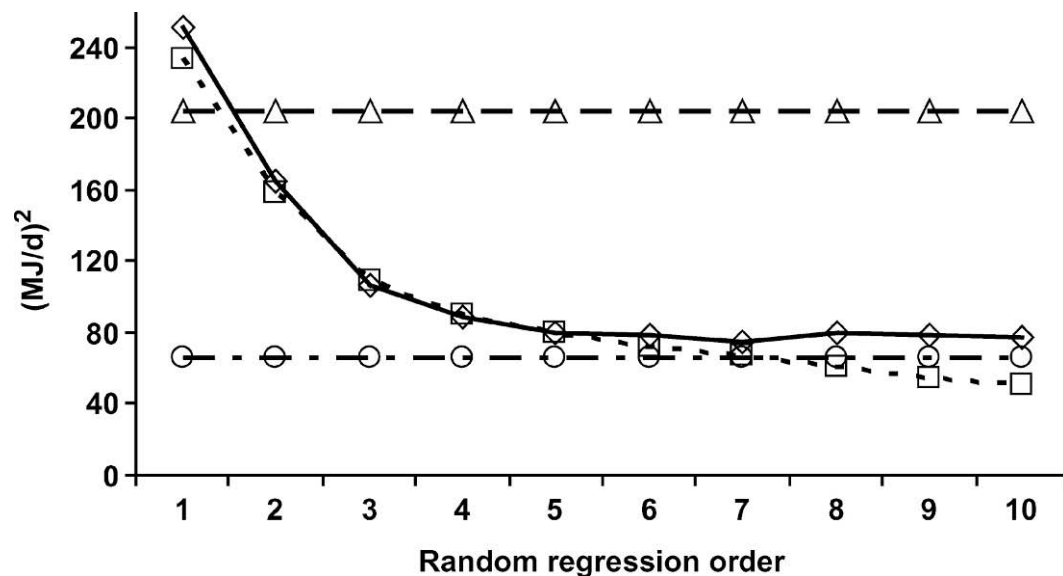


Figure 4. Residual variance estimate of daily energy balance (EB1) predicted within lactation with Bessel functions (BF; \diamond), Legendre polynomials (LP; \square), sinusoidal functions (\triangle), and cubic splines (\circ); SE = 0.23–1.13; BF and LP fixed regression order = 6.

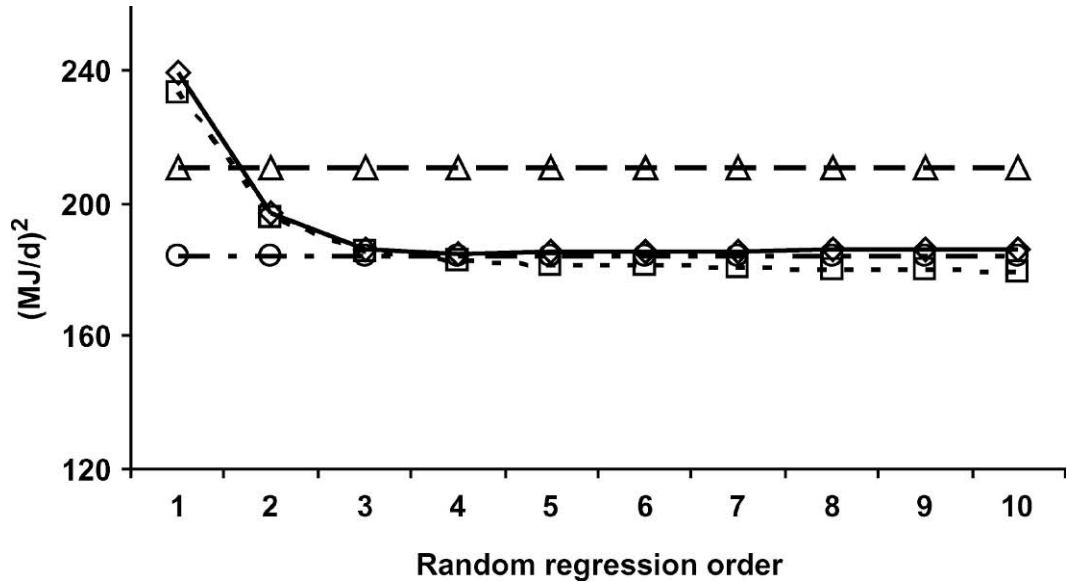


Figure 5. Residual variance estimate of daily energy balance change (EB2) predicted within lactation with Bessel functions (BF; \diamond), Legendre polynomials (LP; \square), sinusoidal functions (\triangle), and cubic splines (\circ); SE = 0.82–1.07; BF and LP fixed regression order = 6.

In Figures 6 and 7, average fitted values across the cows' productive life are fitted. In general, BF, LP, and CS models produced very similar average fit, whereas the model fitting SF fared slightly differently, especially

at the beginning and end of productive life as defined in this study. Figures 8 and 9 show the residual variance of EB1 and EB2, respectively, when the model included sixth-

Table 2. Root mean square error (RMSE), mean absolute difference (ABS), and correlation squared (R^2) between actual daily energy balance (EB1) and predicted with Bessel functions, Legendre polynomials, sinusoidal functions, and cubic splines fitted within and across lactation; BF and LP fixed regression order = 6.

Function	Random regression order	Within lactation			Across lactation		
		RMSE	ABS	R^2	RMSE	ABS	R^2
Bessel function	1	15.8	11.2	0.82	26.5	20.0	0.49
	2	12.8	8.9	0.88	24.9	18.6	0.55
	3	10.2	6.8	0.92	22.9	17.0	0.62
	4	9.4	6.0	0.94	22.9	17.0	0.62
	5	8.9	5.6	0.94	21.1	15.6	0.68
	6	8.8	5.5	0.94	19.8	14.3	0.72
	7	8.7	5.4	0.95	16.4	11.5	0.81
	8	8.7	5.3	0.95	14.6	10.1	0.85
	9	8.7	5.3	0.95	13.8	9.5	0.87
	10	8.7	5.3	0.95	13.4	9.2	0.87
Legendre polynomials	1	15.2	10.9	0.83	24.1	17.9	0.58
	2	12.5	8.7	0.89	22.5	16.4	0.63
	3	10.4	6.9	0.92	21.1	15.3	0.68
	4	9.4	6.1	0.94	19.7	14.0	0.72
	5	8.8	5.6	0.94	18.1	12.7	0.76
	6	8.3	5.3	0.95	16.9	11.9	0.79
	7	8.0	5.0	0.96	15.8	10.9	0.82
	8	7.7	4.8	0.96	14.8	10.3	0.84
	9	7.5	4.5	0.96	14.0	9.6	0.86
	10	7.4	4.4	0.96	13.5	9.3	0.87
Sinusoidal function	—	14.2	9.8	0.85	25.1	19.1	0.55
Cubic splines	—	8.0	5.1	0.95	13.9	9.5	0.86
Standard error		0.09–0.15	0.02–0.05		0.14–0.17	0.03–0.06	

Table 3. Root mean square error (RMSE), mean absolute difference (ABS) and correlation squared (R^2) between actual daily energy balance change (EB2) and predicted with Bessel function, Legendre polynomials, sinusoidal function, and cubic splines fitted within and across lactation; BF and LP fixed regression order = 6.

Function	Random regression order	Within lactation			Across lactation		
		RMSE	ABS	R^2	RMSE	ABS	R^2
Bessel function	1	15.4	10.2	0.48	18.0	12.6	0.29
	2	14.0	8.6	0.57	17.5	12.2	0.33
	3	13.6	8.2	0.60	17.2	11.8	0.36
	4	13.5	8.2	0.60	16.6	11.2	0.40
	5	13.5	8.2	0.60	15.9	10.6	0.45
	6	13.5	8.2	0.60	15.4	10.2	0.48
	7	13.5	8.2	0.60	15.0	9.8	0.51
	8	13.5	8.2	0.60	14.5	9.3	0.54
	9	13.5	8.2	0.60	14.1	8.8	0.57
	10	13.5	8.2	0.60	14.0	8.7	0.57
Legendre polynomials	1	15.2	10.0	0.50	17.6	12.2	0.32
	2	13.9	8.6	0.58	17.3	11.9	0.35
	3	13.5	8.2	0.60	16.8	11.4	0.39
	4	13.4	8.1	0.61	16.3	10.9	0.42
	5	13.4	8.0	0.61	15.9	10.6	0.45
	6	13.3	8.0	0.62	15.4	10.2	0.48
	7	13.3	8.0	0.62	15.1	9.8	0.50
	8	13.3	8.0	0.62	14.6	9.3	0.54
	9	13.2	8.0	0.62	14.3	8.9	0.56
	10	13.2	8.0	0.62	14.1	8.8	0.57
Sinusoidal function	—	14.5	9.3	0.55	17.5	12.4	0.33
Cubic splines	—	13.5	8.1	0.61	14.2	8.9	0.56
Standard error		0.17–0.18	0.03–0.04		0.15–0.19	0.03–0.05	

order fixed regression on BF or LP and random regression on the same functions of order ranging from 1 to 10. Fixed regression of sixth order is used here for illustration purposes. Results were not affected by the order of the fixed regression. Residual variances of SF and CS fitting models are also shown in Figures 8 and 9. For either trait, residual variance was significantly

($P < 0.05$) smaller when the model fitted CS or LP or BF of random order >8 . Smaller residual variance estimates suggest a better fit. These 3 models were not significantly ($P < 0.05$) different from each other. In EB1 analysis, models fitting LP outfitted BF up to random regression order of 6; results were similar for the 2 functions at higher random regression order. In EB2

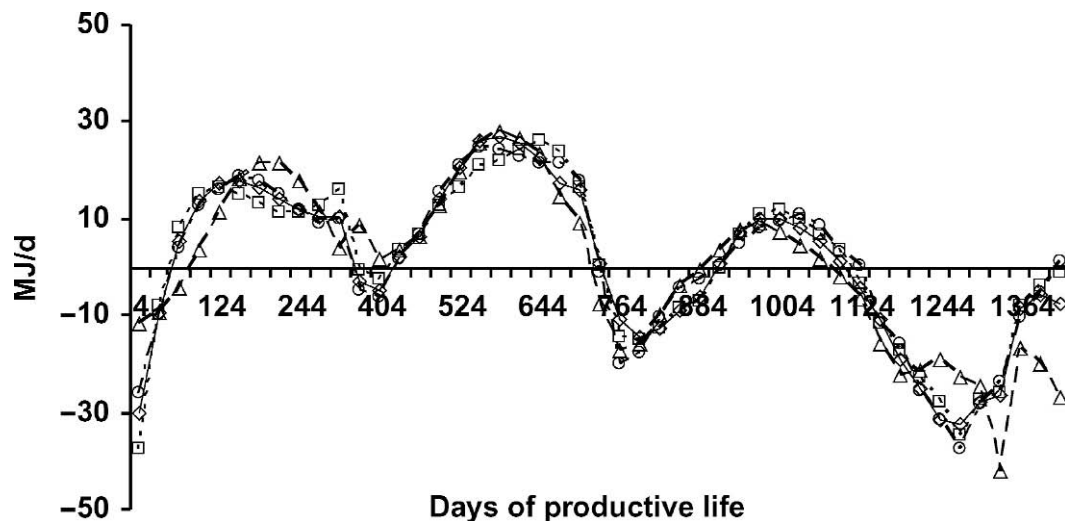


Figure 6. Average daily energy balance (EB1) predicted across productive life with Bessel functions (BF; ◇), Legendre polynomials (LP; □), sinusoidal functions (△), and cubic splines (○); BF and LP fixed and random regression order = 6.

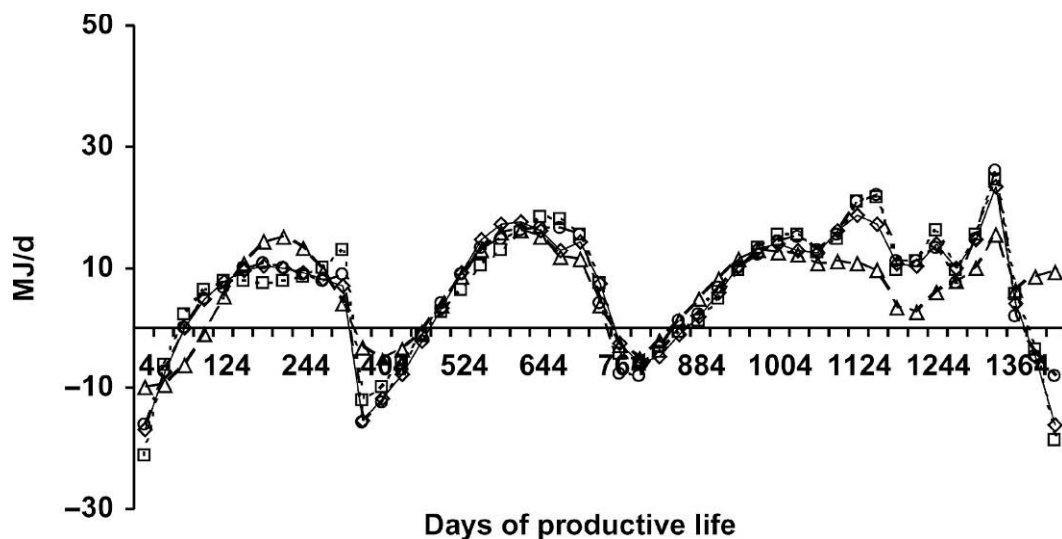


Figure 7. Average daily energy balance change (EB2) predicted across productive life with Bessel functions (BF; \diamond), Legendre polynomials (LP; \square), sinusoidal functions (\triangle), and cubic splines (\circ); BF and LP fixed and random regression order = 6.

analysis, LP and BF gave the same results independently of the random regression order. For both traits, models fitting SF and single random order LP or second random order BF had the largest residual variance.

A very similar picture was painted by comparisons between predicted and actual daily body energy balance (Table 2 for EB1 and Table 3 for EB2). The same comparison criteria as for within-lactation analyses were considered here. Models with CS or LP or BF of random

regression order >8 were associated with the smallest ($P < 0.05$) root mean square error and average bias for either trait. The same models explained the largest proportion of the total phenotypic variance. Differences were more pronounced for EB1 than for EB2.

In all cases, the fit of within-lactation analysis was better than that of across-lactation analysis. This may be attributed to the fact that energy balance measurements were discontinuous across lactation, as they did

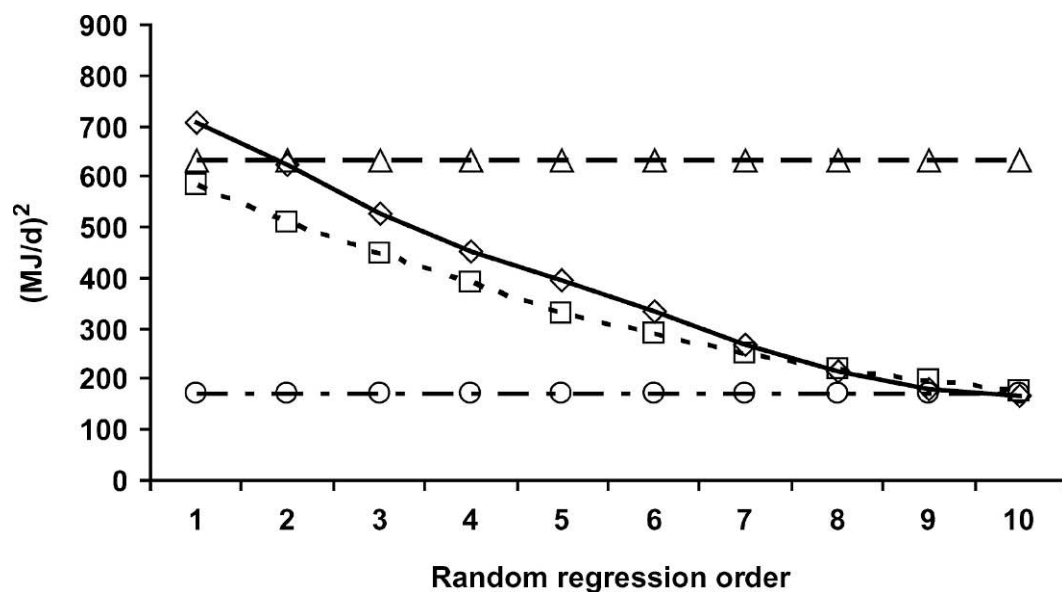


Figure 8. Residual variance estimate of daily energy balance (EB1) predicted across productive life with Bessel functions (BF; \diamond), Legendre polynomials (LP; \square), sinusoidal functions (\triangle), and cubic splines (\circ); SE = 0.76–2.81; BF and LP fixed regression order = 6.

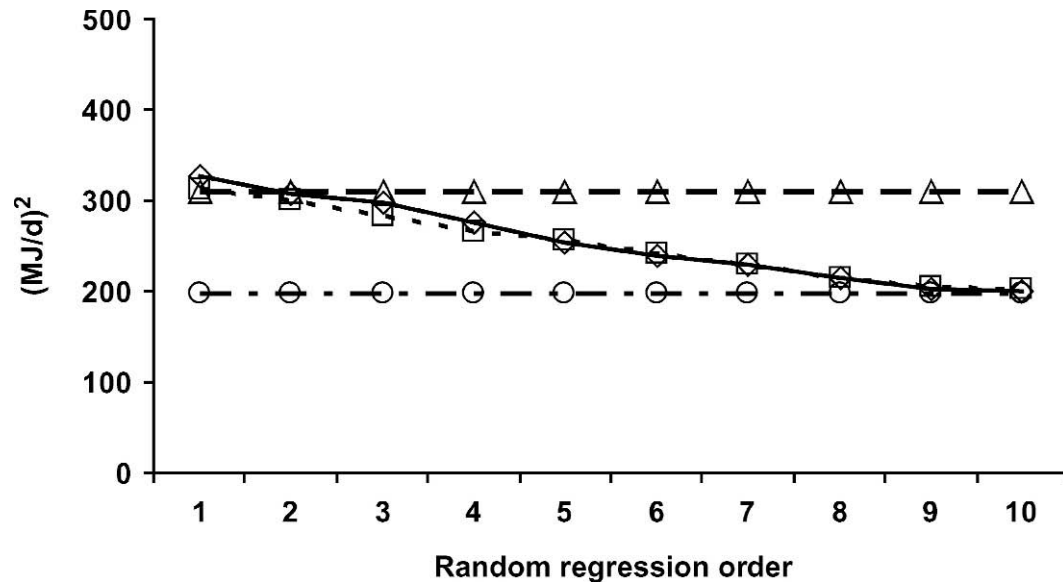


Figure 9. Residual variance estimate of daily energy balance change (EB2) predicted across productive life with Bessel functions (BF; ◇), Legendre polynomials (LP; □), sinusoidal functions (△), and cubic splines (○); SE = 0.76–2.81; BF and LP fixed regression order = 6.

not include observations past d 305 of lactation and the dry period.

DISCUSSION

The objective of this study was to evaluate models for the analysis of daily energy balance of lactating dairy cows at various stages of production. The underlying motive was to enhance the understanding of the way daily energy balance changes within a cow's lactation as well as over its productive life. Benefits envisaged from this work include the identification of appropriate models for future genetic evaluation of animals for energy balance and of models that use energy indicators in early productive life to predict energy balance and associated traits in later lactations.

Energy balance was modeled both within and across lactation, the latter reflecting the energy profile across a cow's productive life. The suitability of within-lactation analysis for this type of data is attested by data discontinuity as they only pertain to the first 305 d of each lactation. No data beyond d 305 of lactation were fitted while there was no information from the dry period. Previous energy balance modeling studies (De Vries et al., 1999) also fitted within-lactation curves. However, cows at the same stage of lactation may be on a different actual day of productive life, depending on calving age and interval. Across-lactation analyses recognize the fact that, from a biological standpoint, there is no discontinuity in the trait as cows are constantly moving from losing energy to gaining it and vice versa. Model-

ing energy balance changes over a cow's productive life would help predict the future energy profile from early life indicators. With appropriate selection strategies, this would assist in preventing excessive body energy loss before it happens. For high-yielding Holstein cows with the genetic propensity to partition nutrients in favor of milk production, it is preferable to prevent loss rather than try to recover excessive energy loss.

In this study, 2 energy balance traits were defined based on combinations of smoothed preadjusted records for milk yield, feed intake, live weight, and BCS. Milk yield and feed intake were recorded daily, whereas live weight and BCS measurements were taken every 7 d. The first energy balance trait, EB1, was calculated from milk yield and feed intake solutions, and exhibited a smooth curve throughout the 3 lactations. The second trait, EB2, was based on live weight and BCS solutions, and its curve was not quite as smooth (Figure 1). This was because EB2 calculations were based on lipid and protein weight changes as predicted from changes in live weight and BCS. This method, however, requires an estimate of the gut fill of the cow (Coffey et al., 2001), which, in turn, is based on the metabolizable energy content of DM intake on the day of measurement. Because consecutive live weight and BCS measurements were actually 7 d apart, variation of daily feed intake in the days between measurements was not fully accounted for. This caused the observed unsystematic oscillations in daily EB2 measures, leading to less-than-smooth curves. As a result, models evaluated here fitted EB1 well but did not provide as good a fit for EB2. In

fact, whereas the best models predicting EB1 explained 96% (within-lactation analysis) and 87% (across-lactation analysis) of the total phenotypic variance, the best models fitting EB2 accounted for 62 and 57% of the variance, respectively.

For data considered in this study, models fitting LP of minimum random regression order 8 for EB1 and 5 for EB2 were the best at describing within-lactation energy balance curves. Higher order (>8) LP along with same order BF and CS provided the best fit to across-lactation energy balance curves. However, the best fit of across-lactation models was significantly ($P < 0.05$) inferior to the best fit of within-lactation models. Lowest within-lactation residual variance estimates were $50 \pm 0.3 \text{ MJ}^2$ for EB1 and $180 \pm 0.8 \text{ MJ}^2$ for EB2. For across-lactation analyses, these estimates were 167 ± 0.8 and $197 \pm 0.9 \text{ MJ}^2$, respectively. Apparently, higher-order across-lactation functions will be needed to reach the same levels of fit as within-lactation analysis, because the former is associated with potentially larger numbers of inflection points and because data are discontinuous. High-order functions, however, render models too complicated and, despite their statistical interest, they may depart from ascribing true biological meaning to the results.

In all cases, CS fitted at equally spaced knot points provided a good fit relative to the other functions, especially when energy balance was modeled across lactation. The way splines are formed makes them and their first 2 derivatives continuous over the length of the curve, possibly resulting in a good fit of the lifetime curve despite the obvious gaps occurring between d 305 and the onset of the following lactation. Bessel functions, in the face of their apparent popularity in various fields of physics, did not fare any better than conventionally used polynomials or splines, at least as far as results of this study were concerned. Finally, sinusoidal functions provided the worst fit in all cases. Although they are harmonic, their symmetrical nature renders them unsuitable for the analysis of data where considerable variation between animals in both amplitude and phase is expected.

The number of animal solutions estimated by each function varied. For models fitting LP and BF, the number of solutions that had to be estimated per cow ranged from 2 to 11, depending on the random regression order. For CS fitted to 12 to 16 knot points (optimal fit), the number of solutions per cow was 10 to 14, respectively. Finally, for SF models, 3 solutions had to be estimated per cow. Although the number of random effects was not exactly the same in all cases, the range was narrow enough, especially with regards to CS and high (recommended) order LP and BF; therefore, the number of

random effects is not expected to have had any serious impact on the results.

Only data from the first 305 d of each lactation were considered in this study. Smooth preadjusted records were available for these days for the 4 individual traits used to calculate energy balance, namely milk yield, feed intake, live weight, and BCS (Coffey et al., 2002). An effort to include more days of lactation resulted in inappropriate values for EB1 and EB2 for days beyond 305. An attempt to account for remaining milking days and the dry period was made by fitting the difference between a cow's calving interval and 305 into the model. The effect was significant ($P < 0.05$) in all cases.

From a practical point of view, EB2 is a more interesting measure of energy balance because it is based on traits that can be routinely recorded in the commercial cow population. Body condition scoring forms an integral part of the official national conformation recording scheme in the United Kingdom, and live weight can be predicted from conformation traits (Koenen and Groen, 1998; Coffey et al., 2003). Thus, random regression models considering repeated daughter observations per sire may be implemented to compute sire genetic evaluations for energy balance change per day of lactation (Coffey et al., 2003). Because feed intake records are not available at the national level, metabolizable energy content of DM intake, required to calculate gut fill, should be inferred from average experimental values, in such a case. Functions evaluated in this study suggest that models fitting LP of order no greater than 5 are appropriate for genetic evaluation within lactation. The complexity of such models should be easy to accommodate computationally for both variance component and breeding value estimation.

In this study, energy balance data were based on smoothed preadjusted milk yield, feed intake, live weight, and BCS records. The main advantage was that sources of systematic variation specific to each of these 4 traits were properly considered. Another advantage was that EB2 measures, based on weekly records, were now available for each day of lactation. The disadvantage was that dependent variables were based on partially regressed values; therefore, their real variance might not have been captured fully. An alternative course of action may be to combine the raw (unadjusted) phenotypic records for the 4 traits to form energy balance measures before analysis. This warrants further research.

CONCLUSIONS

Legendre polynomials provided the best fit to the energy balance traits considered in this study. Within-lactation curves of energy balance based on daily milk

yield and feed intake records were best described by models fitting Legendre polynomials of minimum order 8. The same function of order 5 provided the best fit to an energy balance measure defined as the change in lipid and protein weight predicted from live weight and BCS. These models can be used to calculate genetic evaluations and predict future energy balance from early life measures. High order (>8) Legendre polynomials, along with same order Bessel functions and splines, best modeled the 2 energy balance traits across the cows' productive life (3 lactations). Even higher order across-lactation functions will be needed to reach the same levels of fit as within-lactation analysis, but this might be more statistically than biologically meaningful.

ACKNOWLEDGMENTS

This work was financed by Avoncroft Sires Ltd., BOCM Pauls Ltd., CIS, Cogent, Dartington Cattle Breeding Trust, Genus Breeding Ltd., Holstein UK, National Milk Records plc, RSPCA, and DEFRA in the Sustainable Livestock Production LINK program and based on data collected under a grant from the Scottish Executive Environment and Rural Affairs Department (SEERAD). Contribution of data from the Langhill Dairy Cattle Research Centre, Scotland, is gratefully acknowledged. Ross McGinn is acknowledged for looking after the data.

REFERENCES

- Ali, T. E., and L. R. Schaeffer. 1987. Accounting for covariances among test day milk yields in dairy cows. *J. Dairy Sci.* 67:631–644.
- Arfken, G. 1985. Bessel Functions. Pages 573–636 in *Mathematical Methods for Physicists*. 3rd ed. Academic Press, Orlando, FL.
- Beam, S. W., and W. R. Butler. 1998. Energy balance, metabolic hormones, and early postpartum follicular development in dairy cows fed prilled lipid. *J. Dairy Sci.* 81:121–131.
- Coffey, M. P., G. C. Emmans, and S. Brotherstone. 2001. Genetic evaluation of dairy bulls for energy balance traits using random regression. *Anim. Sci.* 73:29–40.
- Coffey, M. P., G. Simm, and S. Brotherstone. 2002. Energy balance profiles for the first three lactations of dairy cows estimated using random regression. *J. Dairy Sci.* 85:2669–2678.
- Coffey, M. P., G. Simm, W. G. Hill, and S. Brotherstone. 2003. Genetic evaluations of dairy bulls for daughter energy balance profiles using linear type scores and body condition score analyzed with random regression. *J. Dairy Sci.* 86:2205–2212.
- Coffey, M. P., G. Simm, J. D. Oldham, W. G. Hill, and S. Brotherstone. 2004. Genotype and diet effects on energy balance in the first three lactations of dairy cows. *J. Dairy Sci.* 87:4318–4326.
- Collard, B. L., P. J. Boettcher, J. C. M. Dekkers, D. Peticlerc, and L. R. Schaeffer. 2000. Relationships between energy balance and health traits of dairy cattle in early lactation. *J. Dairy Sci.* 83:2683–2690.
- De Vries, M. J., S. Van Der Beek, L. M. T. E. Kaal-Lansbergen, W. Ouweltjes, and J. B. M. Wilmink. 1999. Modelling of energy balance in early lactation and the effect of energy deficits in early lactation on first detected estrus postpartum in dairy cows. *J. Dairy Sci.* 82:1927–1934.
- De Vries, M. J., and R. F. Veerkamp. 2000. Energy balance of dairy cattle in relation to milk production variables and fertility. *J. Dairy Sci.* 83:62–69.
- Emmans, G. C. 1994. Effective energy: A concept of energy utilization applied across species. *Br. J. Nutr.* 71:801–821.
- Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, and R. Thompson. 2002. *ASREML User Guide*. Release 1.0. VSN International Ltd., Hemel Hempstead, UK.
- Green, P. J., and B. W. Silverman. 1994. *Nonparametric regression and generalized linear models*. Chapman & Hall, London, UK.
- Kendrick, K. W., T. L. Bailey, A. S. Garst, A. W. Pryor, A. Ahmadzadeh, R. M. Akers, W. E. Eyestone, R. E. Pearson, and F. C. Gwazdauskas. 1999. Effects of energy balance on hormones, ovarian activity, and recovered oocytes in lactating Holstein cows using transvaginal follicular aspiration. *J. Dairy Sci.* 82:1731–1740.
- Koenen, E. P. C., and A. F. Groen. 1998. Genetic evaluation of body weight of lactating Holstein heifers using body measurements and conformation traits. *J. Dairy Sci.* 81:1709–1713.
- Leach, W. M., Jr. 1989. Electroacoustic-analogous circuit models for filled enclosures. *J. Audio Eng. Soc.* 37:586–592.
- Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling. 1992. *Bessel Functions of Integral Order and Bessel Functions of Fractional Order, Airy Functions, Spherical Bessel Functions*. Pages 223–229 and 234–245 in *Numerical Recipes in Fortran: The Art of Scientific Computing*. 2nd ed. Cambridge University Press, Cambridge, UK.
- Reiss, H. R., and V. P. Krainov. 2003. Generalized Bessel functions in tunneling ionization. *J. Phys. A Math. Gen.* 36:5575–5585.
- Roura, P., J. Fort, and J. Saurina. 2000. How long does it take to boil an egg? A simple approach to the energy transfer equation. *Eur. J. Phys.* 21:95–100.
- Taylor, J. B. 1974. Relaxation of toroidal plasma and generation of reverse magnetic field. *Phys. Rev. Lett.* 33:1139–1144.
- Veerkamp, R. F., J. K. Oldenbroek, H. J. Van der Gaast, and J. H. J. Van der Werf. 2000. Genetic correlation between days until start of luteal activity and milk yield, energy balance and live weights. *J. Dairy Sci.* 83:577–583.
- White, I. M. S., R. Thompson, and S. Brotherstone. 1999. Genetic and environmental smoothing of lactation curves with cubic splines. *J. Dairy Sci.* 82:632–638.